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THE ORIGIN OF THE MAMMALS.

SPECULATIONS as to the origin of the various existing groups of animals and plants are always dangerous, and yet they have for many a certain fascination. They partake, somewhat, of the nature of an algebraic problem in that there are unknown quantities to be discovered, but they differ from any such soluble problem in that we have not equations enough to allow us accurately to ascertain the values of x, y, z and the like. Here is a chance for the play of the imagination and a chance for close guessing at the values of some of the unknown elements. Different students have assigned different values to them, and hence the varying character of the answers we have had given to us. Recall the different forms which we have been asked to consider as ancestral to the vertebrates—cœlenterates, nemertines, annelids, *Phoronis*, crustacea, arachnids, tunicates, *Balanoglossus!* Certainly there has been some error in the assignment of values to the unknown to produce such discordant results as these.

Yet these speculations have a certain value; they call attention to problems, they suggest lines of research, they are exercises of the logical powers. One of these genealogical problems is that which deals with the origin of the mammals. It has been twice 'settled,' and yet there is some new evidence, and there are new points of view.

Until 1884 the general opinion among those who speculated on phylogenetic matters was that the group of mammals had an amphibian ancestry. Huxley was especially prominent in advocating such a line of descent, basing his conclusions upon the naked, scaleless skin, the double occipital condyle and other cranial features, some of which will be mentioned later. Yet this view was not universal, since Owen, in 1876, and Cope, in 1878 and in later papers, had suggested a reptilian ancestry for the group. Still, these speculations attracted but little attention until 1884, when Caldwell's famous dispatch, 'Monotremes oviparous, eggs meroblastic,' excited the enthusiasm of the British Association for the Advancement of Science, then meeting in Montreal. At that date embryology was the ruling force in deciding questions of phylogeny, and the discovery by Caldwell that the *Echidna* laid eggs, and that these eggs were like those of the reptiles rather than those of the amphibia in their segmentation, at once suggested to every zoologist a reptilian ancestry for the mammals. This was still further emphasized a few days later by Cope's paper upon the relations of the theriomorphous reptilia and the monotreme mammalia, read before the American Association at its Philadelphia meeting.

Since that day numerous students have built upon that foundation, and I need but allude to the papers of Cope, Seeley, Osborn, Howes, Lyddeker, Baur and Case, all of which accept the reptiles as the progenitors of the scaleless, hairy, milk-producing vertebrates that we know as mammals. They have brought forward much evidence—but solely osteological in character—in support of their views, and for the summary of this which follows I am largely indebted to the able papers of Osborn.

The particular group of reptiles which they have selected for this high honor is that known as Theriomorphs, the fossils of which are found in rocks of Permian and Liassic age in Illinois, Texas, New Mexico, Scotland, Bavaria, Bohemia, the Urals, Bengal and South Africa. Then they suddenly disappear, for no traces of them occur in rocks of more recent age, and there is a vast gap between them and the earliest mammals of which we have any adequate knowledge. This group shows several features in which they approach the mammalia more closely than do any other reptiles, and a summary of these points may be of value now.

In the mammalia the skull is articulated to the atlas, the first bone of the vertebral column, by a pair of oval articular surfaces, the occipital condyles. These are borne one on each exoccipital bone. In most reptiles, on the other hand, there is but a single condyle, largely or wholly basioccipital in origin. In many of these theriomorphs the exoccipitals partake in the formation of this structure, and in some the basioccipital portion exhibits a tendency to recede, thus exhibiting a condition which, carried still farther, would result in two condyles like those of the mammals.

In the mammals there is a heterodont dentition; that is, there are different kinds of teeth—incisors, canines and molars. In recent reptiles and in amphibia there is no such differentiation, but in these theriomorphs one group presents a dentition which is strikingly suggestive of that of the mammals. Indeed, one species, described from a lower jaw, was at first regarded as a mammal.

In the mammals the anterior dorsal ribs bear peculiar relations to the vertebræ. These ribs bear two 'heads,' by which they are articulated with the backbone. One of these, the so-called tubercular head, articulates with a process, the diapophysis, which arises from the neural arch, while the other, or capitular head, has its articulation with

the bodies or centra of two vertebræ, in such a way as to suggest that its proper place was between them; that is, intercentral in position. This condition has led Cope and others to the view that a vertebral element, the intercentrum, once existed here as it does in many lower vertebrates, and that the rib formerly articulated with this. By the disappearance of this intercentrum the mammalian relations have been brought about. In some of the theriomorphous reptiles the capitular head is also intercentral.

In many mammals there is a small hole, with the disproportionately large name of entepicondylar foramen, in the inner lower end of the humerus, the bone of the upper arm. This opening is for the passage of the brachial artery and the median nerve. In the lower vertebrates such a foramen is unknown, except in the theriomorphs.

Again, in the mammals the lower jaw articulates directly with the cranium by means of a shallow pit, the glenoid fossa, on the ventral surface of the squamosal portion of the temporal bone, no other element intervening between the two. In most of the lower vertebrates the lower jaw does not articulate direct with the cranium, but a movable bone, the quadrate, is inserted between them, and forms a suspensor of the lower jaw. In the theriomorphs and crocodiles the quadrate is fixed and immovable, and is held in position by a second bone, the squamosal, which, together with the quadrate, takes part in the formation of the articulation of the lower jaw. Now, say the advocates of the reptilian ancestry of the mammals, if the quadrate were to become completely fused with the squamosal, the result would give a condition from which the mammalian articulation could readily be derived. In support of this view, they cite the case of a human skull, described by Albrecht, in which a separate bone, which he interpreted as the quadrate, appeared in this very region.

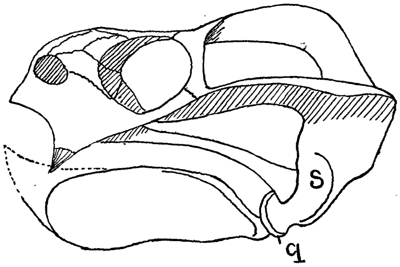

FIG. A. Skull of a Theriomorphous Reptile (*Gordonia*). Showing the quadrate bone (*q*) firmly united to the enlarged squamosal (*s*). After Newton.

Further evidence, which is regarded as pointing in this same direction of a theriomorphous ancestry, is furnished by the pelvis, while the imperfectly known tarsal bones of these reptiles are doubtfully interpreted as supporting the same view. These features, however, are of secondary importance in comparison with those already enumerated, for the peculiarities of the mammalian pelvis and tarsus are as readily derived from the amphibia as from the theriomorphs. The foregoing enumerates the chief osteological evidence for the reptilian ancestry of the mammals. The only other evidence recalled at present which points in the same direction is the character of the segmentation of the monotreme egg, already alluded to.

Within more recent years there has been a tendency upon the part of some zoologists to return to the support of an amphibian parentage of the mammals. Klaatsch, Maurer, Hubrecht and Beddard have pointed out features of the soft parts of mammals, which are more easily interpreted by this assumption; but, of course, this cannot be conclusive, for we can know nothing of these structures in the theriomorphs. Hence this evidence, which will be summarized later, can only be regarded as cumulative and not of first importanee.

The osteological facts which have already been enumerated need analysis, for it is

possible that they will bear another interpretation than that usually accorded them.

The argument from the heterodont dentition can have but moderate value, for we know that different types of teeth have been developed independently in different groups of vertebrates, and it is possible that they could have arisen in the mammals and not have been inherited from the theriomorphs. So, too, with the entepicondylar foramen. The nerve and blood vessels exist in lower forms, and it is conceivable that the existence of the foramen in the two groups may be explained upon the ground of homoplassy and without implying inheritance. This foramen certainly is of too little importance to be used as the basis of great speculations.

The matter of the ribs is more important. In the amphibia with bicipital ribs, the capitular head rests upon the so-called centrum, and not between two centra, as in theriomorphs and mammals. Yet, with our present knowledge, this is far from conclusive, for we know almost nothing of the morphology of the vertebræ in most groups of vertebrates. The researches of Fritsch upon the fossil stegocephalan amphibia have shown that the vertebral centra are by no means simple affairs, but are really composed of several (at least five) separate elements. Traces of at least some of these, more or less distinct, appear in the higher vertebrates; but until the homologies of these are worked out for the existing amphibia, the reptiles and the mammals, arguments based upon the relations of the ribs to centra and intercentra must remain inconclusive. As it stands at present, it must be admitted that the burden of proof, so far as the ribs are concerned, is against the advocates of amphibian ancestry.

The matter of the occipital condyles is even less conclusive. Until the discovery of the theriomorphs, the fact that both amphibia and mammals have two condyles and the sauropsida but one condyle, was regarded by Huxley as the very strongest argument for amphibian ancestry, and the most that is claimed for the double condyles of the theriomorphs is that they show that these animals are not to be counted out upon reasons based upon the articulation between cranium and vertebral column.

Yet in none of these is there an exact reproduction of the mammalian conditions, for in all the basioccipital participates to a greater or less extent in the formation of the condyles, these structures being described at times as distinctly bilobed, at times having the basioccipital portion receded below the level of the rest, but still rather prominent. In other words, the double condylar condition of the theriomorphs—and hence that of the mammals—is supposed to have arisen from the single condyle of other forms by recession of the basi-occipital. In the development of the mammals there are, however, no traces of such a stage. All this, however, is aside from the more fundamental question, Is the occipital region of the skull homologous throughout the vertebrates?

Of far more importance than all these features is the problem of the quadrate. In fact, the whole matter of the ancestry of the mammals may almost be said to hinge upon the decision arrived at as to the fate of the quadrate in the mammals.

A brief review of some points of an anatomical character may make clear the discussion of the quadrate. In the first place, it must be kept in mind—and this is too frequently ignored by those who deal with bones alone—that there are two kinds of bones which differ greatly from each other in history, both ontogenetic and phylogenetic, and that while one may seemingly replace the other, there is no evidence whatever of one passing into the other. These two types are known respectively as cartilage bones and membrane bones. A

cartilage bone is always preformed in the peculiar substance known as cartilage, and in this only later is the chondrin matrix replaced by salts of lime. Membrane bones, on the other hand, never have a cartilage stage. They arise by the direct ossification of connective tissue membranes. Further, investigations seem to show that there may be at least two types of membrane bone, one of which, exemplified by most of the membrane bones of the skull and by the bony plates of the alligator, has arisen by the fusion of the bases of dermal scales or teeth, and the sinking of these to a deeper position. The other type, familiar in the kneepan and the bony strands so well known in the drumstick of the turkey, arises from the ossification of tendons.

In the sharks the skeleton of the jaws arises from a continuous stroma or anlage on either side of the head. Each of these strands—known as the mandibular arch—becomes interrupted in the middle as it becomes converted into cartilage. The upper half of each arch forms the upper jaw—the pterygo-quadrate of anatomy, while the lower half in a similar way gives rise to Meckel's cartilage, the skeleton of the lower jaw. These jaws do not articulate directly with the cranium, but the pterygo-quadrate is suspended in front by ligaments, while behind, besides a ligament, the upper half of the next or hyoid arch intervenes as a hyomandibular element between the jaws and the cranial wall, thus forming a suspensorium for these parts.

In the teleosts, or bony fishes, where bone largely replaces cartilage in the adult, the hyomandibular still acts as a suspensor, while the pterygo-quadrate, relieved of its functions as the upper jaw, ossifies in two portions; in front, as a pterygoid bone; behind as a smaller element, the quadrate. The quadrate articulates, on the one hand, with the hyomandibular; on the other, it supports the Meckelian, the hinge of the lower jaw being formed by the articulation of Meckel's cartilage with the quadrate.

In the vertebrates higher than the fishes the hyomandibular disappears as a suspensor, and it is not to be recognized with absolute certainty in this region. As will be seen shortly, there is some evidence that it is not entirely lost, but persists with changed functions. In contrast to what obtains in the fishes, in amphibia, reptiles and birds, the quadrate articulates directly with the cranium in the region of the ear, and forms a suspensor for the lower jaw. In its history in all these groups the quadrate is preformed in cartilage, and hence, when it ossifies, it becomes converted into cartilage bone. In amphibia, reptiles and birds in the embryonic stages, the Meckelian cartilage, of course, articulates with the quadrate, but when the definitive lower jaw is formed, some features are introduced which must be described. In all the bony vertebrates the Meckelian does not furnish the bones of the lower jaw, but these arise as membrane bones arranged round the cartilage bar. In the amphibia and reptiles the most constant of these bones is a very large, tooth-bearing dentary in front, extending backwards on the outer side of the Meckelian. Further back, on the inner side, is a smaller bone, the splenial, which also may bear teeth. The third of these is the angular, which is placed behind those already mentioned on the lower and inner sides of the proximal end of Meckel's cartilage. The Meckelian ossifies only at its posterior end, where it articulates with the quadrate, giving rise at this point to a cartilage bone, the articular. In short, the lower jaw consists of a single cartilage bone, the articular, and three or more membrane bones.

The articular surface of quadrate and articular presents features which must be mentioned. In all the non-mammalian groups the quadrate has a rounded or some-

what semi-cylindrical surface which fits into a corresponding groove or cavity in the articular.

Another set of bones may be mentioned now. These are the bones of the middle ear, the ossicula auditus of anatomists. It seems probable that the sense of hearing appears in the vertebrates only with the assumption of a terrestrial life, and that the so-called ears of the fishes are organs for the maintenance of equilibrium. In the amphibia, then, true hearing appears. In the salamanders an opening occurs in that part of the cranium which surrounds the inner ear. This opening is the fenestra ovale, and is partly closed by a small cartilage or cartilage bone, the stapes, possibly to be homologized with the hyomandibular already referred to as apparently lacking in the non-piscine vertebrates. This interpretation receives some confirmation from the fact that in several salamanders the stapes articulates with the quadrate, a point which is of importance when we come to a consideration of mammalian structures.

In the frogs, reptiles and birds the stapes is a long slender rod,* frequently called the columella, and is in no way connected with

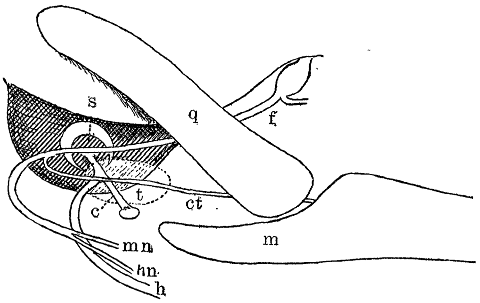

FIG. B. Diagram of Ear Region in a Lizard. *s*, stapes; *c*, columella; *q*, quadrate; *m*, lower jaw; *ct*, chorda tympani nerve.

the quadrate. It rather extends straight outwards from the fenestra ovale, across the cavity of the tympanum, or middle ear, to reach the tympanic membrane. It thus becomes a sound-conducting apparatus, conveying the sound waves across the tympanum to the inner ear. This columella arises in the posterior wall of the tympanum, and, although it later moves forward into the tympanum, must consequently be regarded as a structure belonging to the post-tympanic region.

In the mammals, on the other hand, the sound-conducting apparatus is greatly different. Instead of a columella there is a chain of three bones leading from the fenestra ovale to the tympanic membrane. These are called, in order from within out, the stapes or stirrup bone, incus or anvil, and malleus or hammer, the stapes being situated in the fenestra ovale, the malleus being connected with the tympanic membrane and the incus intervening between these two. Many attempts have been made to homologize these bones with the columella of lower forms, but none of these attempts have been successful, and it is probable that complete homology does not exist. This is shown almost conclusively by two facts of anatomical relationship. In the first place, the middle member of the mammalian chain—the incus—arises in front of the tympanic cavity, and hence cannot correspond to any part of the columella, which, as we have seen, is post-tympanic in origin. Again, the incus lies in front of that branch of the seventh or facial nerve which is known as the chorda tympani, while the columella lies behind it. Now, nerves are older structures than skeletal elements, and any cartilage or bone placed in front of a major branch of a nerve cannot be homologized with a skeletal element lying behind the same nerve in another vertebrate.

Now, if these ear bones of the mammals are not homologous throughout with the columella, with what structures in the lower vertebrates can they be compared?

* The columella is more than stapes, but for present purposes the details are not necessary.

Here embryology comes in to assist. The development of these bones has been followed by many, and it is a rather significant fact that while the embryologists are in substantial agreement in their interpretations, their opinions are at variance with those of the students who have attacked the problem from the stand-

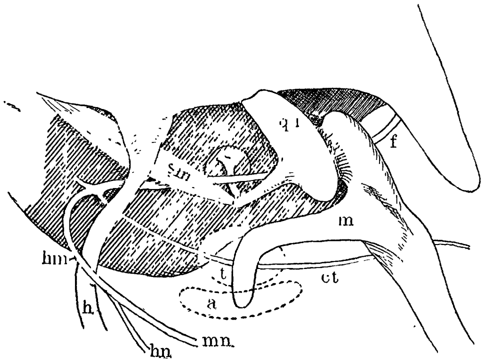

FIG. C. Diagram of the Ear Region in a Mammal. *s*, stapes; *i*, incus; *m*, malleus; *ct*, chorda tympani nerve.

point of adult structure. Now, since the embryologists have the wider view, the larger basis of facts at command, on *a priori* grounds their conclusions should be given the greater weight. Embryology plus comparative anatomy certainly forms a better basis for conclusions than comparative anatomy alone.

In the embryonic mammal, before the appearance of cartilage, a strand of denser mesenchyme extends from the point where the anlage of the stapes can be recognized into the lower jaw. Position and relationships show that this strand is the first appearance of the mandibular arch. With the formation of cartilage this arch becomes divided into a proximal portion, which can be traced, step by step, until it develops into the incus and a more distal portion, which is as clearly Meckel's cartilage, extending into the lower jaw. This incus soon develops an articular surface for connection with the stapes, while a second set of surfaces is found between the incus and the proximal end of the Meckelian cartilage. The incudal surface of this last is convex, while the corresponding articular surface on Meckel's cartilage is concave. It follows from these facts of development and structure, as well as from others which cannot be detailed here, that the incus fulfills, in the embryonic stages, every condition demanded for the quadrate, while the great size of these elements in the early condition can only be interpreted as indicative of some function in their ancestral history different from that of a sound-conducting apparatus. Again, it is a matter of no little importance in what will follow, that this quadrate articulates with the stapes just as in many urodele amphibia, while such relationships are unknown in any reptile, living or fossil. In the third place, this incus for a time articulates directly with the skull, just as does the quadrate in the lower forms, a condition not easily explicable upon any other view than that regarding this as the quadrate.

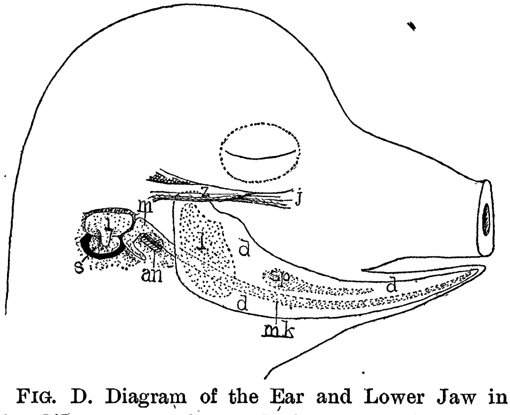

FIG. D. Diagram of the Ear and Lower Jaw in the Pig. *an*, angulare; *d*, dentary; *i*, incus; *j*, jugal; *l*, cartilage of articular region of lower jaw; *m*, malleus; *mk*, Meckelian cartilage; *s*, stapes; *sp*, splenial; *z*, zygomatic process of temporal—the letter lies just in front of the glenoid fossa.

The malleus is largely formed by the ossification of the proximal end of Meckel's cartilage, and this fact, together with every

other relation except one to be mentioned immediately, goes to prove that it is the equivalent of the articular. In the formation of the malleus a membrane bone is concerned. This arises in front of the articular proper on the inner and lower side of the cartilage—that is, in the right position for the angular—and forms the process Folianus of the malleus. At some distance from the malleus two membrane bones form the lower jaw of the adult. The larger of these, from its relations and position, is clearly the dentary, while the smaller and inner one is as plainly the splenial. Thus we can apparently recognize in the mammalian lower jaw the articular and the three membrane bones most constant in the lower vertebrates. In some mammals, according to Parker, two additional membrane bones, each with its equivalent in the lower vertebrates, are said to occur. Besides all these there exists a patch of cartilage in either half of the lower jaw which arises entirely independently of the Meckelian, never unites with it, and which is, so far as I know, without any equivalent in any amphibian, reptile or bird.

To the identification of the bones of the lower jaw which have just been given, there is one very serious objection. The articulation with the cranium is not homologous with that of the lower vertebrates. After the formation of all the bones of the jaw the Meckelian cartilage becomes absorbed between the Folian process and the hinder margin of the dentary, leaving the jaw proper without connection with the quadrate. The posterior portion of the dentary extends up around the second cartilage mentioned, and articulates with the squamosal, the dentary furnishing the articular condyle, the squamosal the glenoid fossa. It is not easy to say how this new articulation can have been introduced, for it is hard to see how an organ in constant use like the jaw could transfer its hinge from the quadrate to the squamosal. And yet, from any point of view, it seems impossible to escape the conclusion that it is not homologous with the articulation of the lower vertebrates, for the articulation in the non-mammalian forms is at the proximal end of Meckel's cartilage, while in the mammals the Meckelian does not come anywhere near the region of the glenoid fossa. Again, in the glenoid fossa there is no trace of any cartilage which could be used as a basis for the view that the quadrate has disappeared at this point.

A word about Albrecht's supposed quadrate may be inserted here, since it has often been quoted in this connection. Albrecht found, on one side of the skull of an idiot, a separate bone in the region of the zygomatic process of the temporal bone, and since the lower jaw articulates at this point, he at once jumped to the conclusion that this bone must be the missing quadrate. Now, the fact that cartilage is unknown in this region would at once negative any such conclusion, while the further fact that the skull in question was that of an imbecile and the additional bone occurred on one side only, is certainly suggestive. No history of the case was given, but it is not beyond the bounds of possibility that an injury to the head may, at the same time, have caused the imbecility and have produced the supernumerary bone, upon which, as a very slender basis, a considerable superstructure of speculation has been built.

There is one series of facts which may possibly lead to an explanation of this change in point of articulation. In certain sharks there occur labial cartilages which lie outside of the jaws and perfectly free from them. Now, the cartilage mentioned above as occurring in connection with the dentary bone of mammals, occupies the position of one of the lower of these labial cartilages—Parker has, indeed, identified

it as a labial—and this has apparently been concerned in the transferrence of the hinge of the lower jaw. This, however, is mentioned only as a suggestion; details have yet to be worked out, and further study may show that this view is untenable.

Now, summing up the evidence of the bones, we may say that the characteristics of the ribs, the heterodont dentition, and the entepicondylar foramen point more strongly towards a reptilian rather than towards an amphibian ancestry for the mammals. On the other hand, the occipital condyles are even stronger evidence in the other direction. But, when we consider the relations of the ear bones and the quadrate, the weight of argument is very strongly opposed to a reptilian ancestry, while these same relations, and especially the articulation of the quadrate with the stapes, go far towards supporting the theory that the mammals have descended from the amphibia.

There is another series of osteological facts which also seems to point in the same direction. In the mammals, as in the amphibia, the ankle joint is formed between the bones of the shank (tibia and fibula) and the proximal row of tarsal bones. In all reptiles of which we have adequate knowledge, the joint is between the proximal and distal rows of tarsal bones—is intratarsal. This, however, is not conclusive, since the foot structure of the theriomorphs is very imperfectly known.

Besides the osteological evidence for the descent of the mammalia from amphibian-like forms, there are facts derived from the soft parts which have a cumulative value. They, however, are not conclusive, for we cannot say what may have been the relations in the theriomorphs. It may be that these extinct reptiles possessed one or all of these features, but the fact that they are lacking in all modern reptiles lends plausibility to the view that they were absent from the older members of the group. A detailed account of these would far transcend the limits of this paper, and but the briefest mention can be made of them.

In the first place, mammals are strongly marked off from all other vertebrates by the existence of hair. For a long time it was thought that hair, feathers and scales were homologous structures, but Maurer has shown that hair is totally different from the others. It is true that Weber has criticised Maurer, but his criticisms seem far from conclusive. According to Maurer—and he offers a large mass of facts in support of his contention—the only structures in the lower vertebrates which can be conceived to have given rise to hair are lateral-line organs of the amphibian type. Now, lateral-line organs are unknown in any terrestrial form. Even in the frogs and salamanders they are lost during the metamorphosis which precedes a life on land. Hence it is very probable that they were lacking in the theriomorphs, all of which were apparently terrestrial in habit.

The student should also read Klaatsch's account of the mesenterial structures, especially of the superior mesenteric artery, to see how impossible it is to derive the relations of these from any known condition in the reptiles. In the mammals these structures are far more primitive than in the reptiles, and Klaatsch concludes that their origins must be sought in forms below the existing amphibia.

Mammals alone have well-developed external ears, and these, as well as the tube leading to the drum—the external meatus—are supported by cartilages. All who have worked at these agree that they must have been derived from opercular structures, like those of fishes, supported by the hyoid arch. Now, all such structures are absent from all known reptiles, nor do we know of them in the amphibia. They must be sought in

forms between the fishes and the stegocephali.

The thoracic duct of the mammals is the primitive lymphatic duct of the left side; that of the right is greatly reduced and receives no lymph from the lower part of the body. Exactly the same conditions occur in the urodeles, but not in the reptiles.

Another item of interest in this connection is that mammals and amphibia get rid of their nitrogenous waste in the form of urea, while reptiles void uric acid.

As we saw earlier, embryology was an important factor in directing attention to the reptiles as ancestors of the mammals, but now the weight of its evidence is in the opposite direction. The fact that the monotreme eggs are meroblastic is far from conclusive, since similar conditions have arisen independently several times in the animal kingdom. Hubrecht, however, has pointed out that certain other features of development — those connected with the fœtal envelopes of the mammals—are not to be derived from the conditions known in any reptile, but that they are easily explained as arising from a type of egg found in the amphibia. As these arguments, so far as I am aware, have not been summarized in English, they may be given in a brief form here, omitting all points which have no immediate bearing upon the question at issue, such as the two types of fœtal circulation, the nutritive functions of the trophoblast and the like.

As is well known, the mammals, like the sauropsida, form a fœtal envelope, continuous with the sides of the body—known as the amnion; and from the fact that the sauropsida are lower than the mammals, the natural view has been that the reptilian type has been the ancestral one, from which that of the mammals has been derived. Were this envelope to arise in all mammals in the same way that it does, for instance, in the sheep or the rabbit, this conclusion could not be gainsaid; but when the amnion of the guinea-pig, the hedgehog, the flying fox and that of man are considered, we meet conditions which it is extremely difficult, if not impossible, to explain in such a way.

Forget for the moment the well-known diagrams of amnion formation which appear in any text-book, for they will confuse. In the hedgehog there arises very early in development a two-layered vesicle, the layers being, according to Hubrecht's interpretation, ectoderm and entoderm. At one end of the vesicle the ectoderm is much thicker than elsewhere, and projects like a cone or papilla into the central cavity. Soon a splitting occurs in this ectodermic thickening, so that the whole structure now forms a double vesicle, its two cavities being separated by a partition formed of ectoderm and entoderm, the larger and older cavity having walls of ectoderm and entoderm, the later one walls of ectoderm alone. From this partition the embryo will arise.

There are now clearly two kinds of ectoderm present in the germ; one the embryonic, the other forming the outer walls of both vesicles. For this latter Hubrecht has proposed the name trophoblast in allusion to its nutritive functions, and he distinguishes two kinds or regions of trophoblast; that of the smaller cavity being called the allantoidan, that of the larger the omphalidian trophoblast, from their future relations to allantoic and vitelline circulations.

With the development of the mesoderm, which, of course, arises between the ectoderm and entoderm of the germinal area, an important change is introduced. The somatic sheet of this layer grows outward and then turns upward into the angle between the embryonic ectoderm and the omphalidian trophoblast, and then bends downward on the inner side of the latter, while the splanchnic mesothelium follows the deeper surface of the entoderm into the

same region. This last, however, has no concern for us at present.

From the angle just mentioned the somatic mesothelium now gradually extends upwards and inwards between the cells of the allantoidan trophoblast as a double sheet, dividing the trophoblast of this region into two layers. Finally, the mesothelium growing in from all sides meets and fuses above the embryo, which now lies in a cavity roofed in by an internal layer of ectoderm and an outer of mesothelium. Between this roof and the trophoblast there is now a space, lined on either wall by mesothelium, and hence clearly a part of the cœlom. The cavity above the embryo is the amniotic cavity, and its ectodermal lining is the amnion. It now shows in every relation exactly the same features as are well known in the chick; but, of course, these are derived in a greatly different way. We see from this that the first splitting in the ectoderm described above is the separation of amnion from the rest of the ectoderm. In the sauropsida and in some mammals, as is well known, the amnion arises in quite a different manner; not by the splitting of the ectoderm, but by the upgrowth and overgrowth of folds from all sides of the embryo—each fold consisting of ectoderm and somatic mesothelium—the folds at last meeting and fusing above the embryo, the final result closely simulating that described for the hedgehog. The question now arises, which of these two modes of amnion formation is the primitive and which the derived condition? Hubrecht's line of reasoning in settling this question is, in outline, as follows: The am-

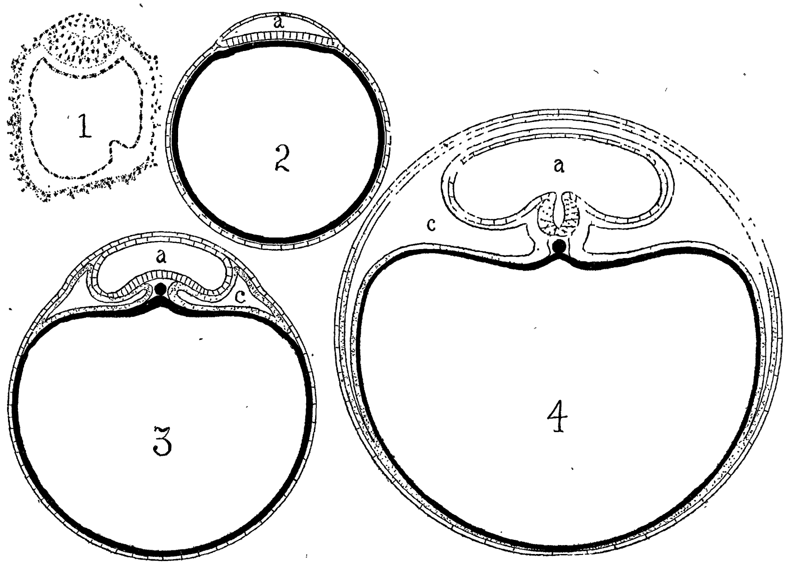

FIG. E. Diagrams of the Origin of the Amnion. 1. Section of an egg of *Erinaceus* after Hubrecht, showing the two layers and a cavity in the ectodermic thickening. 2, 3 and 4, diagrams of successive stages of formation of the amnion; ectoderm white; mesoderm dotted; entoderm black. *a*, Cavity of amnion; *c*, cœlom. 2. Diagram of the stage of Fig. 1, the amniotic cavity formed by splitting of the primitive ectodermic thickening. 3. Appearance of the mesoderm and cœlom, the somatic layer of the mesoderm growing upwards above the amniotic cavity, the roof of which is beginning to split into amnion and serosa. 4. Process of the amnion formation complete, the result closely similar to what is found in reptiles and birds.

nion, filled with fluid and surrounding the embryo, is clearly a protective apparatus. Its origin can in no way be explained by the presence of the large yolk or of an egg-shell, for in the sharks which have both no amnion appears. As a protective apparatus it, of course, would have the greatest value in an embryo developing inside the mother, protecting it, like a water cushion, from the peristaltic and other movements of the mother. Hence, it is more reasonable to look for the origin of the amnion in viviparous rather than in oviparous forms. Now, an amnion formed after the type found in the hedgehog can act as a protection from the very first, while one arising as in reptiles cannot have any protective value until the folds have completely closed over the embryo, and so it is difficult to account for the incipient stages in the reptilian type. Again, it is easy to derive the reptilian condition from that described, while the amnion of the hedgehog or of man is not easily explained on an hypothesis of descent from the reptilian condition. Hence it follows that there is no inherent improbability, and that there is much plausibility, in the view that the amnion formed by splitting is the primitive, that by overgrowth the derived type.

Now, where are there features that could have given rise to such structures? The ancestral form must have been viviparous, and it must have had a two-layered ectoderm. Now, the amphibia fulfill the conditions in both respects, for there are salamanders which bring forth living young, and nowhere in vertebrates, except in the amphibia, do we find a two-layered ectoderm, while here a two-layered condition occurs throughout the group; and further the outer layer does not participate in the formation of the embryo.

In conclusion, it may be said that at present the weight of evidence is in favor of an amphibian ancestry for the mammals, but when the known forms of amphibia are examined none is found which will meet exactly the requirements of the case. The limbless cæcilians are, of course, out of the line; the anura, with their reduced vertebral columns and reptilian ear structures, are equally out of the question. The urodeles approach more nearly to the ancestral form, but their skull is so degenerate that it cannot give rise to the zygomatic arch so characteristic of the mammals. There remains only the group of stegocephala. These are extinct forms, the earliest fossils of which appear in the Carboniferous, the subclass dying out in the Triassic. In every known feature these are closer to what the ancestors of the mammal must have been than are any of the other groups, and yet not a single form of stegocephalan is known which can be said to meet the demands required for the ancestor of the mammals. This ancestor must be some form closely allied to, but yet more primitive than, any known stegocephalan. Further, it may be said that we cannot derive urodeles, cæcilians or anura from any stegocephala as yet discovered.

The earliest known stegocephala are well differentiated and widely distributed, and they have a structure greatly different from that of the crossopterygian ganoids from which they have in all probability descended. The ancestor of the mammals partakes of characters intermediate between those of the crossopterygians and those of the most primitive stegocephalan known, and yet one in which the amphibian characters predominate over the ganoid features.

We must, however, remember that the geological record is as yet imperfectly known. We have as yet found no form which serves to bridge the gap between the finned and the limbed vertebrates. Footprints have been found in Devonian rocks in Pennsylvania which, in the light of our present

knowledge, we can interpret only as those of a stegocephalan, but no hard parts have been found to show us what the animal was like. We may hope, yes, almost expect, that future exploration will show us stegocephalans in rocks of Devonian age; and when those are found it is possible that they will embrace types which will be decisive as to mammalian ancestry. Yet how slight are the chances of such discovery is shown by one fact concerning our knowledge of the mesozoic mammals. Nearly half of the known species of these were found in a bed of clay in southern England, the whole deposit measuring forty feet in length, ten in breadth and five inches in thickness.

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THE RELATION OF PHYSICAL GEOGRAPHY TO OTHER SCIENCE SUBJECTS.*

IN geography we have not as yet reached that stage when vague spheres of influence give place to definite territorial boundaries. Our science is still unorganized, its frontiers are not demarked and the dividing lines of its provinces are not yet drawn. My subject compels me to take up a number of questions still so unsettled that I can hardly hope to suggest even a *modus vivendi* which in this time of boundary disputes will be acceptable in all its details to many besides its author.

At least in America, we shall all agree that physical geography is not identical in its limits with what our English friends term physiography. It is not a summation of our knowledge of nature. Such was the older physical geography, and valuable as was its view over the entire kingdom of science, it was found impracticable as an educational instrument. With its string of disconnected chapters on the elements of physics, chemistry, astronomy, geology, botany, zoology, and ethnology, concluding perhaps with a chapter on precious stones, it is no wonder that there was sometimes applied to it the sacred definition of a circle whose center is everywhere and whose circumference is nowhere. And yet to many a boy it gave his only world-view, his only touch with nature. When Huxley spoke of it, this Erdkunde, as 'a peg on which the greatest quantity of useful and entertaining scientific information can be suspended,' it was not in disparagement; for he termed it one of the essentials of a liberal education.

Physical geography has often been treated as though it were equivalent to the 'science of geography,' as Strachey has defined it, or as synonymous with the 'general geography' of the Germans. But its note is neither the introduction of the causal notion nor a topical treatment of the subject. It is not to be set over against either descriptive or a real geography. Surely the adjective in the phrase may well have a restrictive influence. Either 'physical' as here used is equivalent to 'natural,' in which case our science reverts to physiography, or else it limits the subject to physical as distinct from biologic phenomena. Accepting this restriction, we may set the divisions of geography in the following scheme:

1. Chorographic geography.
2. Physical geography, with its subheads of the geography of the planet, the geography of the air, the geography of the sea, and the geography of the land.
3. Biotic geography, the distribution of animals and plants.
4. Anthropic geography, the geography of man.

The chorographic member, dealing with position, direction and dimension, is the rudiment from which the entire body of geography has developed. The map, its first product, remains its chief vehicle of

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